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Environmental Perturbations Reflected in Internal Shell Growth Patterns of *Corbicula fluminea* (Mollusca: Bivalvia)[1]

by

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Abstract. Anthropogenic and natural seasonal environmental perturbations were reflected in shell growth patterns of specimens of *Corbicula fluminea* living at the northernmost extent of their range along the east coast of North America (Raritan River, New Jersey). Growth of organisms in experimental cages was monitored from August 1981 to January 1982 and from July to December 1982 at stations located upstream (controls: 2 stations) and immediately downstream (perturbed: 1 station) from a combined industrial-sewage effluent. In 1981, the growing shell margin of each clam was notched with a small drill before each was placed in a cage; these marked organisms were sacrificed after various lengths of time. In 1982, specimens were not notched, but a growth cessation mark in the shell microstructure of all caged organisms marked the beginning of the monitored growth period. Growth patterns in shell microstructure were examined in acetate peels and polished thin sections. Microgrowth increments in the outer crossed-lamellar layer were deposited at an average rate of approximately one increment per day. A growth cessation mark found in all specimens sampled in 1981 (n = 53) was dated to within two days of a major storm using increment counts, revealing the accuracy of their use to date shell regions. Lack of growth in winter resulted in a growth discontinuity in the inner complex crossed-lamellar layer and an associated growth cessation mark in the outer layer. Increment counts suggested that growth resumed in late March or early April each year as water temperatures rose above approximately 10°C. Growth rates of 1+ year old individuals during spring and early summer (before entering experimental cages) averaged 65 and 45 μm/increment in 1981 and 1982 respectively. In 1981, growth rates at each site were significantly slower during the monitored growth period than before it, which was probably due to injury inflicted by notching the ventral shell margin. In 1982, growth rates of unnotched clams at the control sites were similar before and after entering the experimental cages (after an initial two-week decrease in growth rates). However, unnotched specimens moved to the perturbed site in 1982 subsequently grew at significantly slower rates and had fewer increments during the monitored period than those collected from cages at control sites.

INTRODUCTION

AQUATIC ECOLOGISTS are frequently concerned with assessing effects of environmental events, such as chronic, periodic, or accidental additions of a pollutant, on growth of organisms after the event has occurred. In the absence of information about pre-disturbance growth rates, the ecologist, like the paleontologist, is confronted with the problem of after-the-fact data acquisition. Detailed analyses of growth patterns in molluscan shell structure provide a tool for addressing this problem. Records of an organism's dynamic environment are capable of being preserved as structural, morphological, or chemical changes in the shell. Research into these relationships has been largely to reconstruct paleoenvironments (PANNELLA & MACCLINTOCK, 1968; RHOADS & PANNELLA, 1970; BERRY

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& Barker, 1975; Pannella, 1976; Jones, 1980; Rye & Sommer, 1980; Lutz, 1981; Dodd & Crisp, 1982). However, implications of this approach for ecological work have also interested many neontologists (Rhoads & Pannella, 1970; Kennish & Olsson, 1975; Kennish, 1980).

Present knowledge of the relationship between the environment and bivalve shell structure is limited. However, studies of shell growth patterns of *Mercenaria mercenaria* (Linné) by Kennish & Olsson (1975) and Kennish (1980) have demonstrated the application of shell analytical techniques to *in situ* environmental monitoring studies. In the present study, microstructural shell growth patterns of the freshwater Asiatic clam *Corbicula fluminea* (Müller) were analyzed to assess effects on clam growth of the combined effluents of an organic chemical plant and a sewage treatment facility in a freshwater, non-tidal segment of the Raritan River, New Jersey. *Corbicula fluminea* was chosen as the test organism because it maintains a large population within the river (Trama, 1982), has rapid rates of shell growth (Britton *et al.,* 1979; Britton & Morton, 1982), and because it is an opportunistic, pest species (Britton & Morton, 1982). In order to discern the effects of environmental perturbations in shell microstructure, it was necessary to first document the natural, seasonal shell growth pattern of the species.

The shell of *Corbicula fluminea* is composed of three calcareous layers when viewed in radial section. These are, from exterior to interior: the outer fine crossed-lamellar layer, a pallial myostracum, and the inner complex crossed-lamellar layer (Taylor *et al.,* 1973; Counts & Prezant, 1982; Prezant & Tan-Tiu, 1985). Cursory examination of thin radial sections (or acetate peels) of the aragonitic outer and inner layers reveals bands or lines within the shell (Figure 1A, B). A single pair of dark lines within the outer layer that delineates a lighter band of shell between them is defined as a microgrowth increment. A growth cessation mark is an irregularity in the periodic deposition of microgrowth increments, often resulting in a V-shaped notch in the shell exterior, an unusually thick microgrowth increment boundary, or an abrupt change in the depositional surface, caused by a loss of mantle attachment to the ventral margin (Kennish & Olsson, 1975; Richardson *et al.,* 1980). Furthermore, growth lines within the inner layer, which are often associated with microgrowth increments or growth cessation marks in the outer layer, may also reflect the growth history of the animal.

Trama (1982) first reported the occurrence of *Corbicula fluminea* in the Raritan River from collections made in March 1981. He estimated the year of introduction as not later than 1978 based on an age of between 3 and 4 years for the largest specimen collected, which had a shell length of 25 mm. Little is known about the population ecology of *C. fluminea* in the Raritan River. Based on other studies in North America and Asia (see reviews of Britton & Morton, 1979, 1982), *Corbicula* can aptly be described as opportunistic, but also well adapted, especially in its reproductive biology, to lotic environments. Density-independent factors, such as weather and reservoir drawdown, have been shown to cause catastrophic mortalities of *Corbicula* in streams, lakes, and reservoirs, but due to early maturation and high fecundity, the organism has been able to maintain populations in many such systems (Britton & Morton, 1979). The temperature ranges for survival and growth of *C. fluminea* are not precisely known, but Rodgers *et al.* (1979) reported a minimum of 10°C for growth. Low winter temperatures and their duration are suspected of limiting the spread of the species to generally south of latitude 40°N on the North American continent. Maximum shell lengths of *Corbicula* in North America vary from a low of 18 mm in San Luis Reservoir, California, to between 40 and 50 mm in other systems in Texas and California, suggesting that factors other than low winter temperatures are involved in controlling ultimate shell size (Britton & Morton, 1982). The relatively small maximum size of *Corbicula* attained in the Raritan River, New Jersey, then may indicate that this population is "dwarfed," and possibly stressed by factors other than low winter temperatures.

To study shell growth during known periods, caged populations of *Corbicula fluminea* were established near the effluent discharge and at two control stations in the Raritan River in summer 1981 and sampled, along with the natural population, during the next one and one-half years (Figure 2). Through comparisons of microstructural shell growth of caged *C. fluminea* at the three locations and uncaged specimens at one site, we (1) analyzed effects of chronic exposure to the effluent on growth, (2) determined effects of notching the ventral shell margin and caging on growth, (3) documented the natural annual pattern of shell growth (from which changes caused by the effluent, notching and(or) caging had to be distinguished), and (4) determined the periodicity of microgrowth increment formation.

MATERIALS AND METHODS

Sampling Methods

Caged populations of *Corbicula fluminea* were established at three stations in the Raritan River, New Jersey (Figure 2). The experimental station, AC, received the combined effluents of the American Cyanamid Organic Chemical Plant and the Somerset-Raritan Valley Sewage Authority. Composition of the effluent varied considerably on a daily basis (B. Ruppel, NJ Department of Environmental Protection, personal communication). Consequently, we did not determine the specific effects on shell growth of high nutrient loadings or organo-chlorine compounds in the effluent, but rather the integrated results of chronic exposure to a broad spectrum, sublethal alteration of water quality. Only a small population of *C. fluminea*

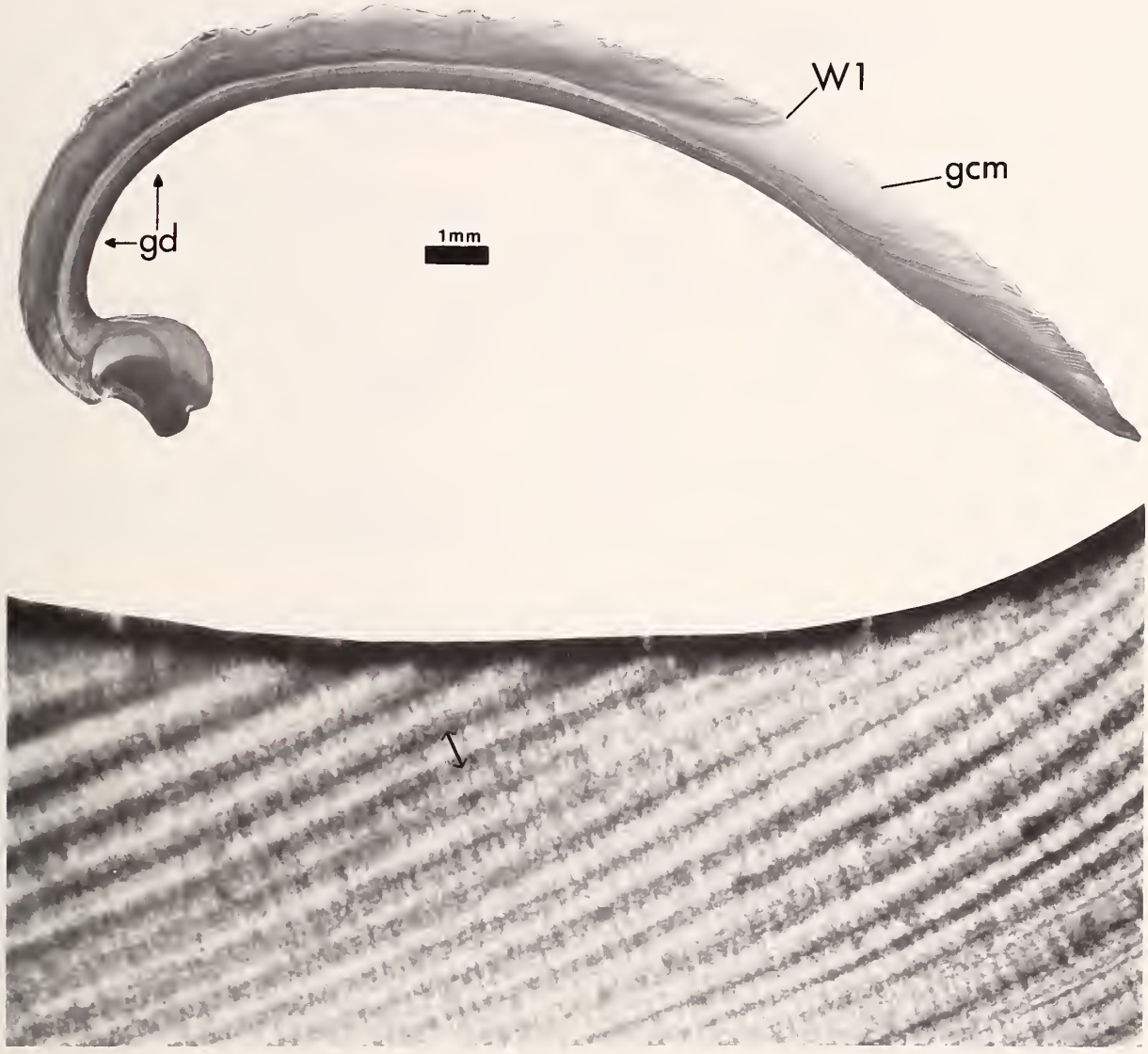

Figure 1

A (above). Photographic enlargement of a thin shell section of a specimen of *Corbicula fluminea* collected on 13 July 1981 from the natural population at station C (see Figure 2). Print was made by placing thin shell section in an enlarger and exposing photographic paper directly; thus, the enlargement is a negative image of the section. The winter 1980–1981 growth cessation (W1) and the growth cessation mark (gcm) in the outer fine crossed-lamellar layer, and the growth discontinuity (gd) in the inner complex crossed-lamellar layer are labelled. Total shell height is 18.1 mm and growth is to the right. B (below). Light micrograph of the outer fine crossed-lamellar layer of a specimen of *Corbicula fluminea* showing a series of microgrowth increments. Arrows delineate one increment. Micrograph is a positive image of the section. Growth is to the right and the horizontal field width is 0.7 mm.

was present at station AC, but a large population, with shell lengths ranging from 2 to 20 mm, was located at the confluence of the Millstone and Raritan rivers (Trama, 1982; this study), approximately 1.6 km upstream from station AC. This site was one of the controls (station C) and was the source of all animals placed in cages at the three stations. The other control station, DI, located 12 km upstream from station AC, was selected because there were no direct inputs to the site from sewage treatment plants, industries, or landfills. Station DI in 1981 did not have a natural population of *C. fluminea* associated with it. In 1982, the station was moved approximately 500 m upstream where clams were found in numbers similar to those at station AC.

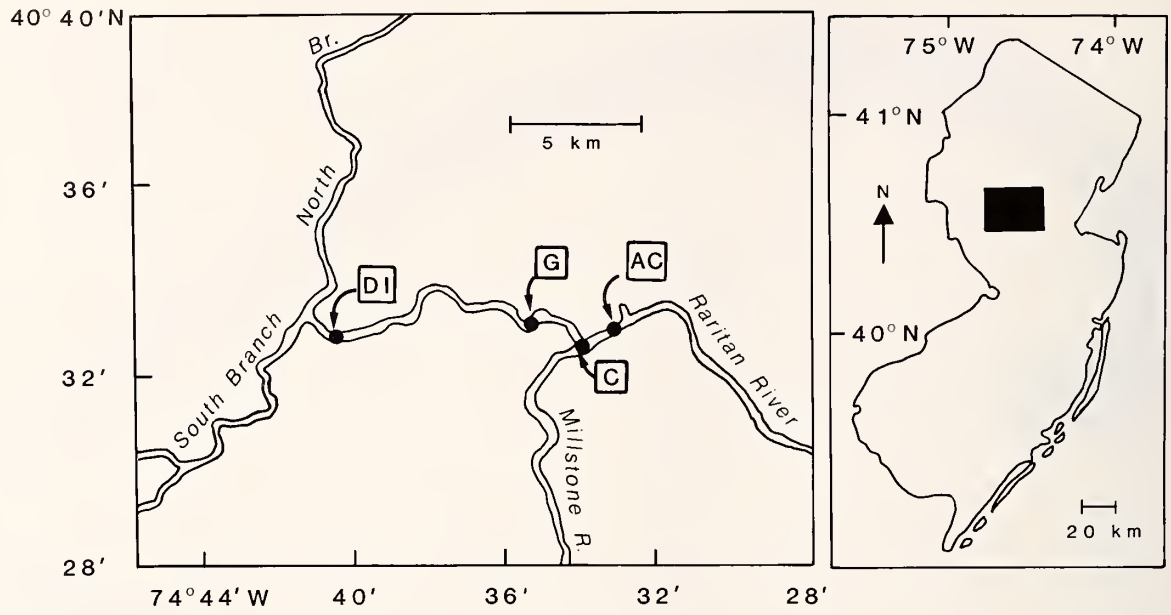

Figure 2

Map of New Jersey, U.S.A. (right); shaded area is enlarged on the left. Stations: AC, experimental site; C, control site and location of natural population; DI, control site; G, United States Geological Survey (USGS) gauging station at Manville, NJ.

Two groups of caged specimens of *Corbicula fluminea* (shell lengths ranging from 8 to 20 mm) were established and sampled in 1981. The first group, Notch I, consisted of animals collected on 17 August 1981. The ventral margin of each animal was notched with a drill (bit size of 1.6 mm) to provide a reference point on the shell prior to planting in cages at stations DI and AC (one cage per station). Cages were 0.3 × 0.3 × 0.15 m open wood frames lined with 1 mm galvanized steel mesh. Substratum from each site was placed in the cage to a depth of approximately 10 cm and 50 specimens of *C. fluminea* were planted in each cage, a density of 530 clams per m^{-2}. The second group, Notch II, was composed of animals collected on 16 September 1981 and notched as described for Notch I. For this group, cages consisted of plastic mesh (1.6 mm) bags filled with substratum from each station and anchored to the bottom. Fifty clams were placed in each bag, yielding the same cage densities as the Notch I group. One cage with Notch II specimens was placed at the two control stations (DI and C) and one perturbed (AC) station. Samples of Notch I and II animals were collected and sacrificed on five and three occasions, respectively, through January 1982. There were massive mortalities of *C. fluminea* in spring 1982 in all cages, as well as in the natural population at station C. To continue the experiment, new animals were collected from the rejuvenated population at station C.

In 1982, cages were constructed and sampled by Dr. Angela Cristini as part of a study of the use of adenylate energy charges to detect stress (Cantelmo-Cristini *et al.*, 1983). Shells of caged and uncaged specimens were supplied to us by Dr. Cristini. Cages were 0.9 × 0.9 × 0.25 m wood frames, with the top, bottom, and a portion of two opposing sides (0.9 × 0.1 m openings) composed of 1.6-mm mesh cloth. Two cages were placed at each site. Substratum from station C was placed in each cage to a depth of 0.2 m. On 19 July 1982, approximately 200 clams were placed in each cage, a density of 250 clams per m^{-2}. The ventral shell margin of these animals was not notched. Three animals were sampled from the cages at each station and the natural population at station C on six dates through December 1982.

Examination of Shell Growth Patterns

A single valve from each specimen was embedded in epoxy resin and radially sectioned (along the height axis from umbo to ventral margin). The two cross-sectional surfaces were finely ground with 600-grit carborundum powder, polished with diamond compounds on lapidary wheels, etched for 30 secs in 0.9 N HCl, rinsed in distilled water, and air-dried; one was used to prepare an acetate peel replica of the microstructural growth patterns (Kennish *et al.*, 1980) while the other was used to prepare a thin shell section (Clark, 1980).

To determine the periodicity of microgrowth increment formation, the number of microgrowth increments (mean of three counts) in specified regions of the shell was de-

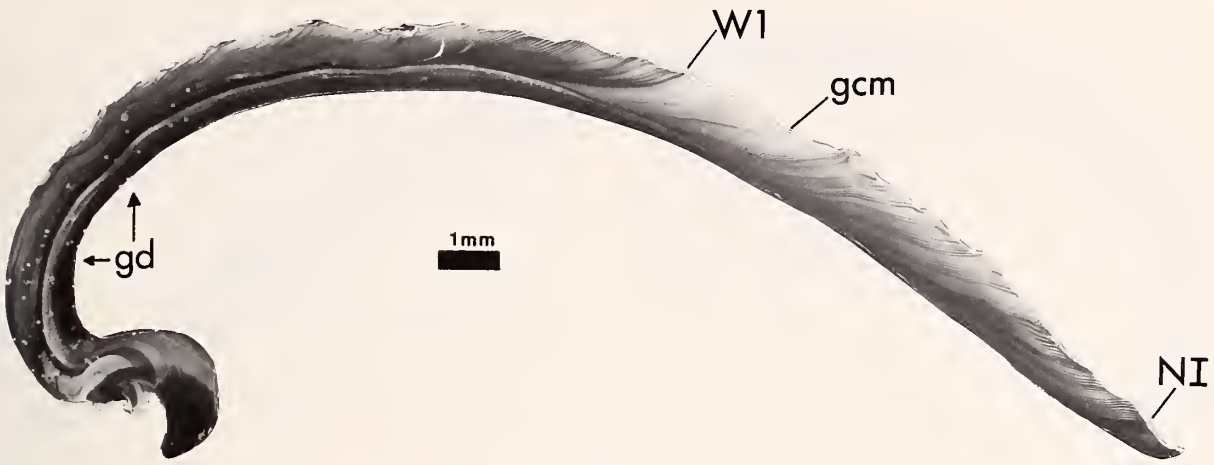

Figure 3

Photographic enlargement of a thin shell section of a specimen of *Corbicula fluminea* from the Notch I group collected from station DI on 19 September 1981. Clam was notched on 17 August 1981 (NI). Total shell height is 19.6 mm. All other features are as in Figure 1A.

termined using the acetate peel under a compound microscope at 100× magnification. Counts were made in shell regions in which the dates at the beginning or end of the count, or both, were known. The distance (in μm) between the two points was measured along the shell exterior surface, which is the surface of maximum growth (SMG) (Pannella & MacClintock, 1968) in radial shell sections. Measurements were made from either the peel or thin section using a compound microscope (at 40×) equipped with a calibrated ocular reticle. The shell height corresponding with the beginning and(or) endpoints of an increment count was measured to the nearest 0.1 mm using either (1) a pair of calipers using the unembedded valve of each specimen, or (2) an ocular reticle at 40× using the acetate peel or thin section. Height measurements were chord distances from the umbo to the shell exterior surface along a straight line between the two points and not along the shell exterior surface. Statistical procedures used (analysis of variance, least-squares linear regression, Student's *t*-test and Kruskal-Wallis test) were those of Sokal & Rohlf (1969).

RESULTS

Natural Shell Growth Patterns

Collections in 1981

Notching the ventral shell margins of clams on 17 August (Notch I) or 16 September 1981 (Notch II) produced a growth cessation mark, NI or NII, in each radial section (Figures 3–5). The notch divided each shell section into regions deposited before (toward the umbo, or dorsal) and after (toward the shell margin, or ventral) it. Exact location of the growth cessation mark caused by notching was aided by the location of the V-shaped notch on the exterior shell surface.

In 25 of 44 Notch I and 28 of 32 Notch II clams (or 53 of 76 clams sectioned in 1981), there was a recognizable series of microgrowth increments in the outer layer and two growth lines within the inner layer (Figure 3; see also Figure 1A). A growth cessation mark (W1) formed the ventral boundary of the group of microgrowth increments, and was associated with one growth line in the inner layer. Another growth cessation mark (GCM) in the outer layer, located between 1.2 and 3.7 mm ventral from W1, was associated with the other growth line. The growth lines within the inner layer will hereafter be referred to as discontinuities, because, as it will be shown, each resulted from a period of little or no shell growth.

There are two lines of evidence supporting the hypothesis that the series of microstructures described above was formed between late fall 1980 and spring 1981. First, Notch I and II clams without growth discontinuities in the inner layer were an average of 6.9 and 4.2 mm smaller in shell height, respectively, at the time of notching than those with discontinuities (Table 1A). Mean shell heights of clams without discontinuities, 9.1 mm in mid-August (Notch I) and 12.4 mm in mid-September (Notch II), could be attained by young-of-the-year, or the spring 1981 brood (Britton & Morton, 1979). These shell heights were similar to those at mark W1 in clams with discontinuities (Table 1B). These data suggest that clams with the series of microgrowth increments in the outer layer and growth discontinuities in the inner layer were members of the 1980 year-class. Winter 1980–1981 was represented as growth cessation mark W1 and an associated discontinuity in the inner layer. No clams in either the Notch I or II groups had other growth discontinuities in the inner layer or growth cessation marks in the outer layer that would correspond with winter 1979–1980; thus, all clams were most likely either members of the 1980 (1

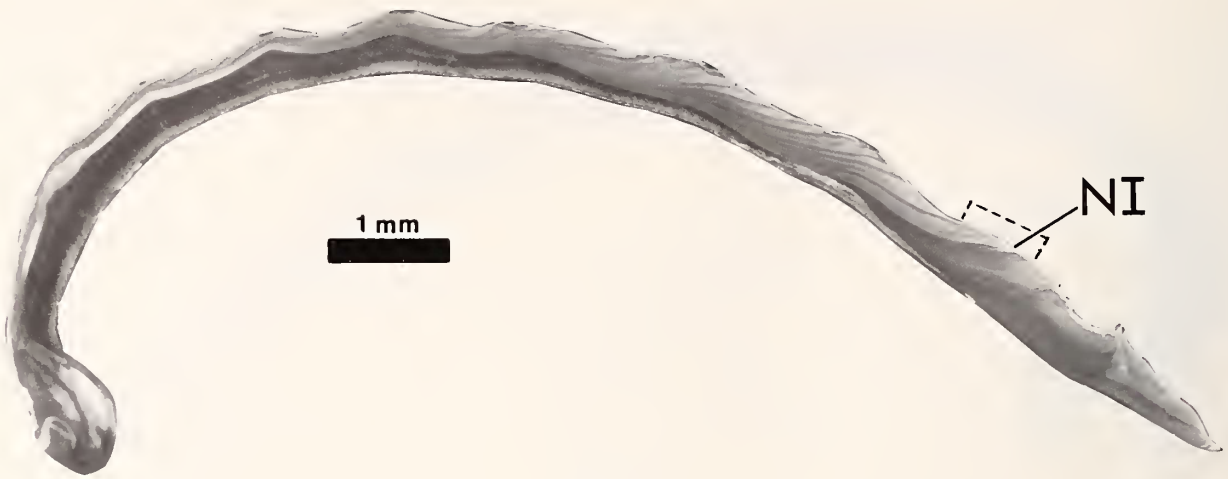

Figure 4

Photographic enlargement of a thin shell section of a specimen of *Corbicula fluminea* from the Notch I group collected from station DI on 14 November 1981. Clam was notched on 17 August 1981 (NI). Total shell height is 10.2 mm. Dashed lines mark portion enlarged in Figure 5. All other features are as in Figure 1A.

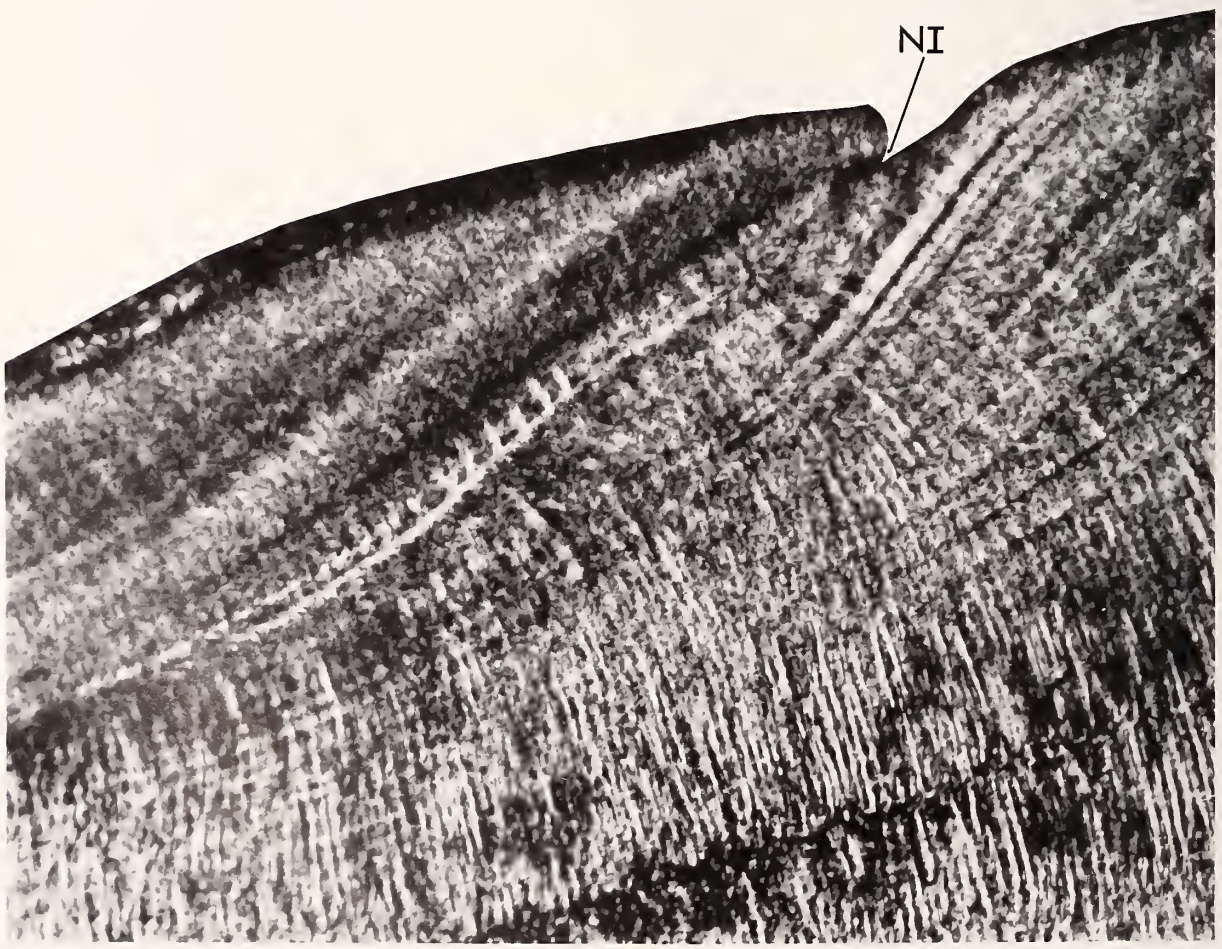

Table 1

Shell height (mm) at the notch (Table 1A) and at the winter 1980–1981 growth cessation (W1; Table 1B) in Notch I (notched on 17 August 1981) and Notch II (notched on 16 September 1981) groups of *Corbicula fluminea* with and without growth discontinuities (GD) in the inner shell layer. Collections from all dates and stations were pooled.

		With GD			Without GD	
Group	N	Mean	Range	N	Mean	Range
A. Shell height (mm) at notches						
Notch I	25	16.0	12.3–19.1	19	9.1	6.3–12.3
Notch II	28	16.6	13.1–19.2	4	12.4	11.1–13.5
B. Shell height (mm) at W1						
Notch I	25	8.8	4.2–12.3			
Notch II	28	9.0	5.0–11.3			
Total	53	8.9	4.2–12.3			

year old; Figure 3) or 1981 year-class (young-of-the-year; Figure 4).

The second group of data that aids in dating the microstructures described above was microgrowth increment counts and measurements of shell growth between W1 and NI or NII. Data obtained from these shell regions (and from clams sampled in 1982) suggest that microgrowth increments were periodically deposited, because the number of increments was independent of the amount of shell deposited by both Notch I ($r^2 = 0.02$) and Notch II ($r^2 = 0.18$) clams (Figure 6). The mean number of increments from W1 to NI or NII in each group suggested an average deposition rate of approximately one increment per day. Data obtained from clams moved to the three stations and notched on the same day were pooled because there were no significant differences in shell growth (Kruskal-Wallis test: Notch I: $H = 0.71$, $P > 0.1$; Notch II: $H = 4.18$, $P > 0.1$) nor in the mean number of increments counted (Notch I: $t = 0.01$, $P > 0.9$; Notch II: $F = 2.35$, $P > 0.1$) among clams in each group (Table 2). In Notch I clams, the grand mean (±95% confidence interval) number of increments from W1 to the notch was 136.3 (±6.2). If one increment were formed each day, the "mean" date of growth resumption after W1 would be 3 April, or 136 days before 17 August. Similarly, the grand mean number of increments in Notch II clams was 160.5 (±5.5), placing the "mean" date of growth resumption on 9 April, or 160 days before 16 September. These two independent estimates of the date of growth resumption are quite similar, and for purposes of this discussion, the grand "mean" date of growth resumption in spring 1981 is 6 April, or halfway between the two dates. Further support for an average daily deposition rate of microgrowth increments was seen in the difference in mean number of increments from W1 to each notch (24.2), which was similar to the number of days between notch dates (30; Figure 6).

Resumption of growth in early April 1981 might also have been predicted on the basis of the water temperature record for the Raritan River and the reported temperature tolerances of *Corbicula fluminea* (Rodgers *et al.*, 1979). From late November 1980 to late March 1981, water temperatures near station C were 7°C or below (U.S. Geol. Survey Water-Data Report NJ-81-1, 1982). A prolonged period of valve closure and inactivity could be reflected in the shell as a growth discontinuity and cessation mark as in Figures 1A and 3 (see Lutz & Rhoads, 1977). Between 25 March and 7 April 1981, water temperatures near station C increased from 7 to 12°C (Figure 7), which could have stimulated shell deposition. The close agreement between the estimated date of growth resumption from increment counts and the water temperature record supports both of the following hypotheses: (1) discontinuance of growth in winter 1980–1981 was reflected in shell microstructure as a discontinuity within the inner layer and W1 in the outer layer, which followed deposition of a recognizable series of microgrowth increments in fall 1980, and (2) microgrowth increments in the outer layer were formed at an average rate of one per day from W1 to each notch.

Assuming that winter 1980–1981 was reflected in shell microstructure as in hypothesis (1) above, then GCM was formed subsequently, possibly during spring 1981 (Figures 1A, 3). As can be seen in Figure 7, the mean daily discharge of the Raritan River near station C increased over 50-fold, from 6.3 to 342.6 $m^3 \cdot sec^{-1}$, from 10 to 12 May 1981 as a result of 10 cm (4 inches) of rain in the Raritan River watershed. This was the highest mean daily flow recorded during the two-year study period. Based on increment counts from W1, GCM could have resulted from the increase in turbidity and high flow rates associated with this storm. As in the shell region from W1 to each notch, the number of increments from W1 to GCM was independent of the amount of shell deposited ($r^2 =$

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Figure 5

Light micrograph of the portion of outer fine crossed-lamellar layer outlined in Figure 4 showing the growth cessation mark resulting from notching on 17 August 1981 (NI). Note the narrow microgrowth increments deposited after (to the right of) the growth cessation mark, as well as the greater proportion of "crossed-lamellar" microstructures. Growth is to the right and the horizontal field width is 0.7 mm.

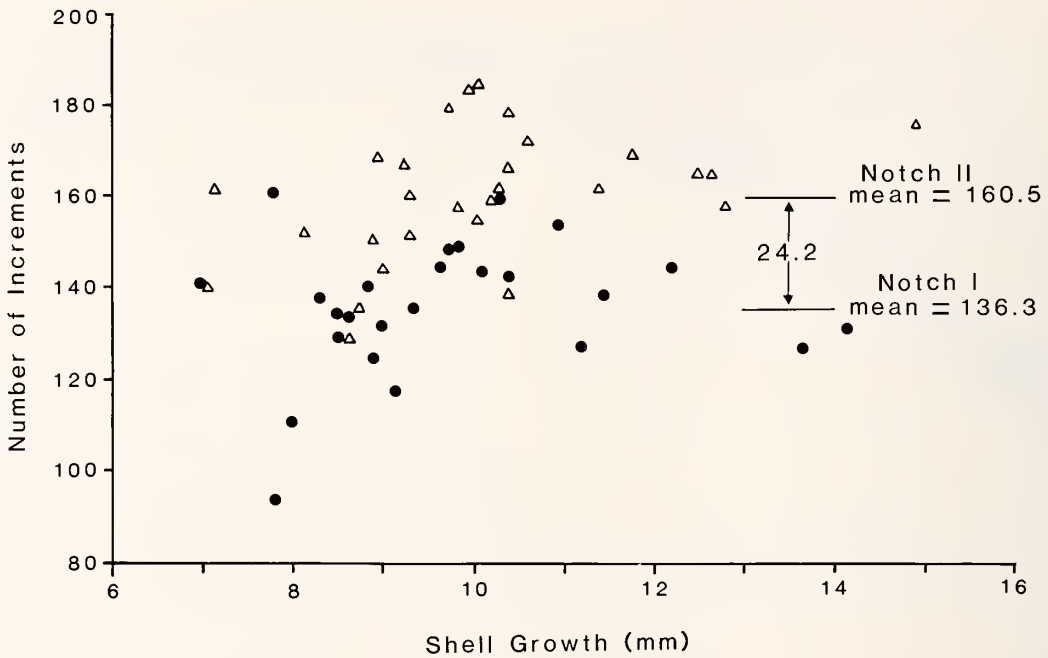

Figure 6

Number of microgrowth increments in the outer layer of Notch I (solid circles) and II (open triangles) groups of *Corbicula fluminea*, from W1 (see Figure 1) to the notch, as a function of shell growth (see Table 2). The mean numbers of increments in each group are shown, along with the difference between the two means.

0.0003; Figure 8). There were no significant differences in the mean number of increments from W1 to GCM in both of the following groups of tests (Table 3): (1) among clams collected from different stations within each notched group (Notch I: $t = 1.02$, $P > 0.2$; Notch II: $F = 0.09$, $P > 0.75$), and (2) between separately pooled Notch I and II clams ($t = 1.82$, $P > 0.05$). Pooling increment counts from the 53 Notch I and II clams resulted in a grand mean of 34.3 (±0.9) increments, which placed the date of GCM formation on 10 May 1981, or only two days before the date of highest mean flow.

Average growth rates along the SMG (shell height axis) from W1 to Notch I and II were 69 and 62 μm/increment (day), respectively, with a total range of 44–108 μm/increment. Individual shell length increases from W1 to Notch I and II, when divided by the mean number of increments in each group (136 and 160 respectively) yielded mean daily growth rates of 63 and 55 μm/day along the length axis, respectively, with a total range of 41–87 μm/day. These rates were calculated from clams with initial (at W1) shell heights ranging from 4.2 to 12.3 mm (Table 1), and lengths ranging from 5.6 to 13.6 mm. Post-

Table 2

Shell growth and number of microgrowth increments from W1 to the notch in Notch I and II groups of *Corbicula fluminea* (see Table 1). Collections from all dates were pooled.

			Shell growth (μm)		Number of microgrowth increments		
Group	Station	N	Median	Range	Mean	±95% CI	Range
Notch I	DI	12	9500	8300–12,200	136.3	129.7–142.8	118.0–154.0
	AC	13	8830	7000–14,150	136.2	125.1–147.3	93.7–160.7
	Total	25	9350	7000–14,150	136.3	130.1–142.5	93.7–160.7
Notch II	DI	12	9840	7150–14,920	166.5	157.5–175.5	135.7–185.0
	C	5	8960	8140–10,240	152.3	134.2–170.4	129.3–168.7
	AC	11	10,400	7040–12,800	157.7	149.4–166.0	138.7–178.3
	Total	28	10,000	7040–14,920	160.5	155.0–166.0	129.3–185.0

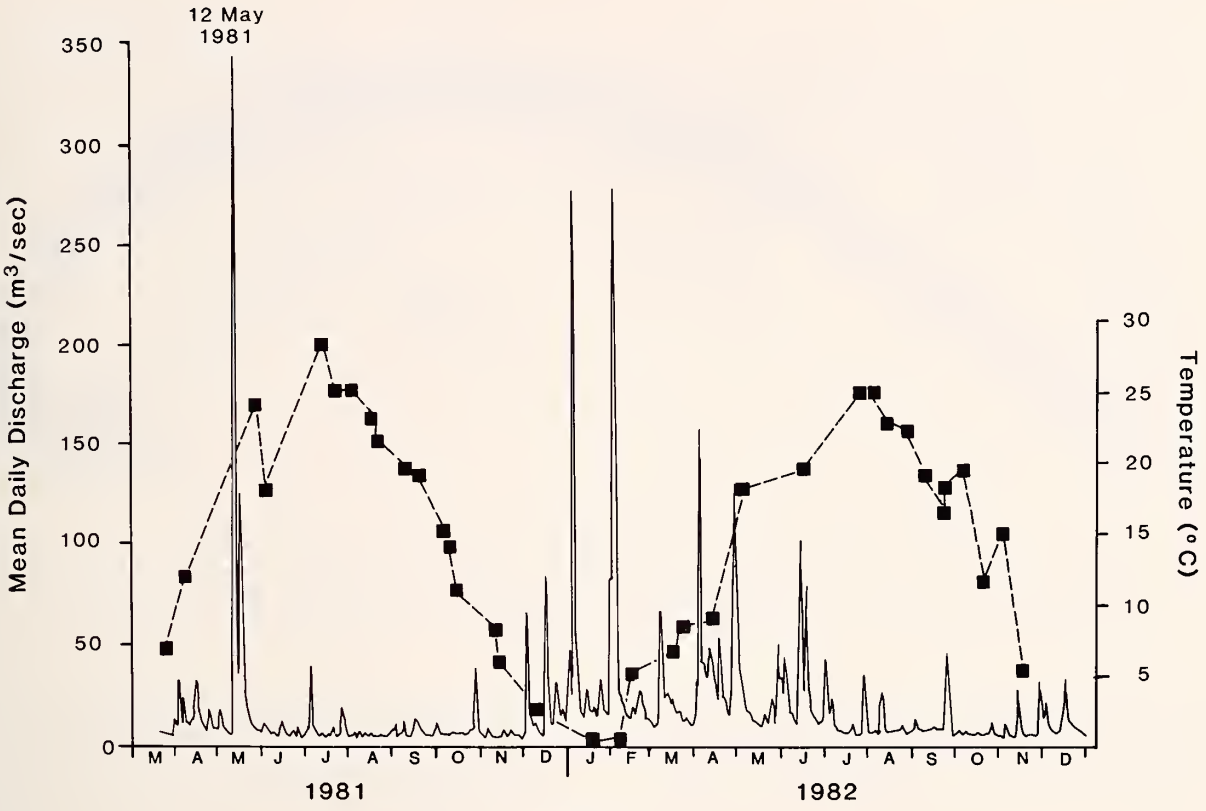

Figure 7

Mean daily discharge (solid line) and water temperature (symbols and dashed line) of the Raritan River at the gauging station at Manville, NJ (see Figure 2). Data from U.S. Geological Survey Water-Data Reports NJ-81-1 and NJ-82-1, and from USGS-WRD, 418 Federal Building, 402 E. State St., Trenton, NJ 08608. Some water temperatures were measured at station C during this study.

notch growth rates along the SMG of Notch I clams declined to a mean of 25 μm/increment (range of 14–44 μm/increment), a decline of over 60% from pre-notch rates regardless of the station to which each clam was moved or the date of collection. Post-notch growth rates of Notch II clams were negligible at all stations and from all collection dates. As will be shown with reference to collections of unnotched clams in 1982, the large decline in post-notch growth rates in 1981 was most likely a result of notching and not an effect of the cage or station to which clams were moved.

Collections in 1982

The growth disturbance mark in shell microstructure caused by moving clams from the natural population at station C to cages at the three stations on 19 July 1982 was less distinct than that caused by notching the ventral margin in 1981. The move was reflected in microstructure as a growth cessation mark (M) that was translucent in thin section. In all specimens moved to control stations DI and C, an opaque region in the outer shell layer was deposited ventral to M (Figure 9). This opaque region was generally not observed in post-move shell growth of clams moved to station AC (Figure 10). Identification of the move disturbance in clams moved to stations DI, C, and AC was based on shell growth measurements and counts of microgrowth increments in shell regions ventral and dorsal to M, as well as its absence in clams collected from the wild population at station C (Figure 11).

Analyses of shell dorsal to M revealed the presence of a single discontinuity in the inner shell layer associated with a recognizable series of two or three growth cessation marks in the outer shell layer of 45 of 50 clams moved to experimental or control stations (Figures 9, 10). This growth pattern was also observed in 14 of 17 clams sampled from the natural population at station C (Figure 11). As with the Notch I and II clams collected in 1981, it will be shown that this series of microstructures was caused by a growth discontinuance in the winter of 1981–1982; clams without this series of microstructures were members of the spring brood of 1982. The ventral-most growth cessation mark in the series of two or three will hereafter be referred to as W2.

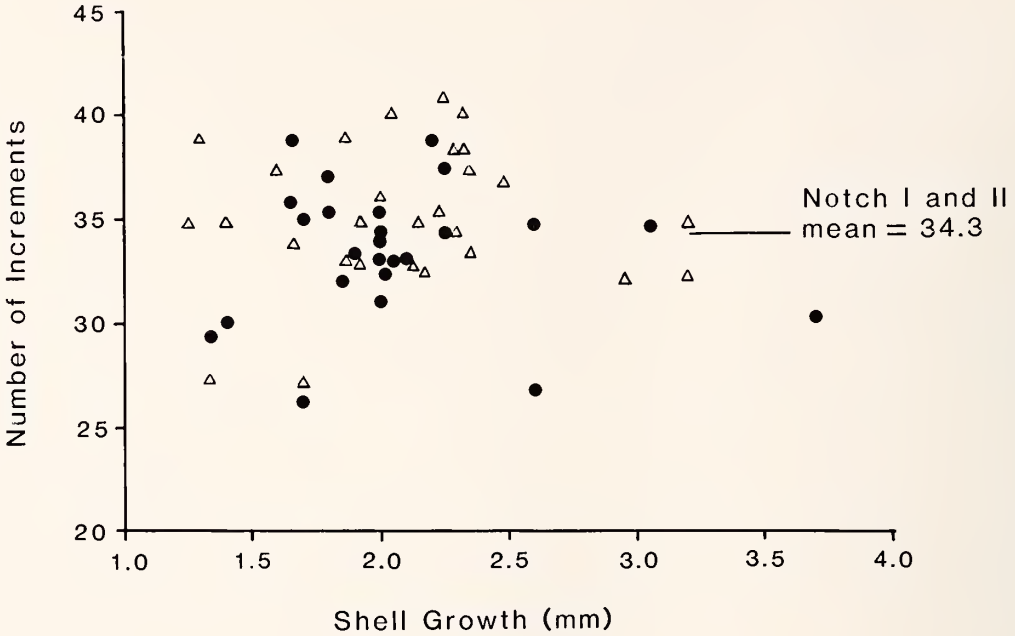

Figure 8

Number of microgrowth increments in the outer layer of Notch I (solid circles) and II (open triangles) groups of *Corbicula fluminea*, from W1 to the growth cessation mark (gcm; see Figures 1B and 3), as a function of shell growth (see Table 3). The mean number of increments for the two groups combined is shown.

Measurements of shell growth and counts of microgrowth increments from W2 to M yielded results similar to those from collections in 1981: (1) there was no correlation between the number of increments and the amount of shell growth ($r^2 = 0.21$; similar in pattern to Figure 6), suggesting that microgrowth increments were periodically deposited, and (2) the mean number of increments from W2 to M suggested an average deposition rate of one increment per day. Data obtained from clams moved to the three stations were pooled because there were no significant differences in shell growth (Kruskal-Wallis test: $H = 1.06$, $P > 0.5$) nor in the mean number of increments counted ($F = 0.07$, $P > 0.75$) among clams in each group (Table 4). Thus, prior to entering the period of monitored growth (or before 19 July 1982), there were no significant differences in growth among the one experimental and two control groups of clams. Using the grand mean of 113.9 (±5.6) increments from W2 to M, placed the "mean" date of growth resumption after winter on 27 March 1982 (114 days before 19 July). Resumption of

Table 3

Shell growth and number of microgrowth increments from W1 to growth cessation mark, GCM (see text), in Notch I and II groups of *Corbicula fluminea* (see Table 1). Collections from all dates were pooled.

			Shell growth (μm)		Number of microgrowth increments		
Group	Station	N	Median	Range	Mean	±95% CI	Range
Notch I	DI	12	2000	1700–2600	34.1	32.1–36.1	26.3–38.7
	AC	13	2000	1350–3700	32.8	30.8–34.8	26.7–38.7
	Total	25	2000	1350–3700	33.4	32.1–34.7	26.3–38.7
Notch II	DI	12	2280	1250–3200	35.4	33.1–37.7	27.0–40.7
	C	5	1660	1300–2350	34.7	31.8–37.6	33.0–38.7
	AC	11	2130	1350–3200	34.9	32.4–37.4	27.3–40.0
	Total	28	2140	1250–3200	35.0	33.7–36.3	27.0–40.7
	Grand total	53	2000	1250–3700	34.3	33.4–35.2	26.3–40.7

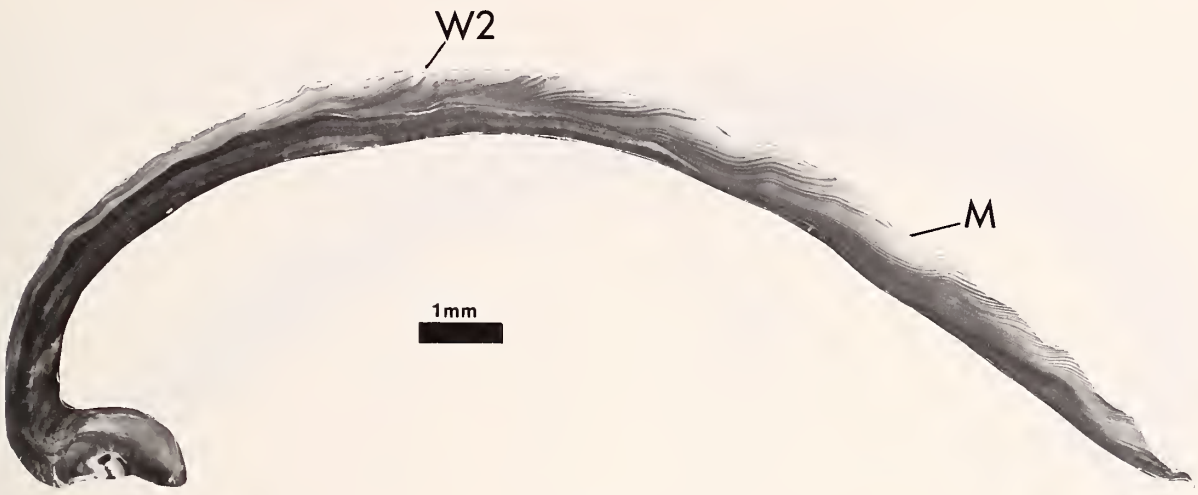

Figure 9

Photographic enlargement of a thin shell section of a specimen of *Corbicula fluminea* collected from the cage at station C on 20 October 1982. Growth cessation caused by moving clam from the natural population to the cage on 19 July 1982 is labelled (M), as is the winter 1981–1982 growth cessation (W2). Total shell height is 14.9 mm; growth is to the right.

growth in late March could also have been predicted from the water temperature record (Figure 7).

The average growth rate along the SMG from W2 to M for the 45 clams was 45 μm/increment (day), with a range of 25–94 μm/increment, or approximately 20 μm/increment less than in 1981. Dividing individual increases in shell length from W2 to M by the mean number of increments (114) yielded a mean daily shell length increase of 46 μm/day, with a range of 28–78 μm/day. These rates were calculated from clams with initial (at W2) shell heights ranging from 4.8 to 10.4 mm and lengths ranging from 6.2 to 11.7 mm.

Shell Growth during Monitored Periods in 1982

Because growth of clams during spring and early summer 1982 was similar in the groups moved to the three

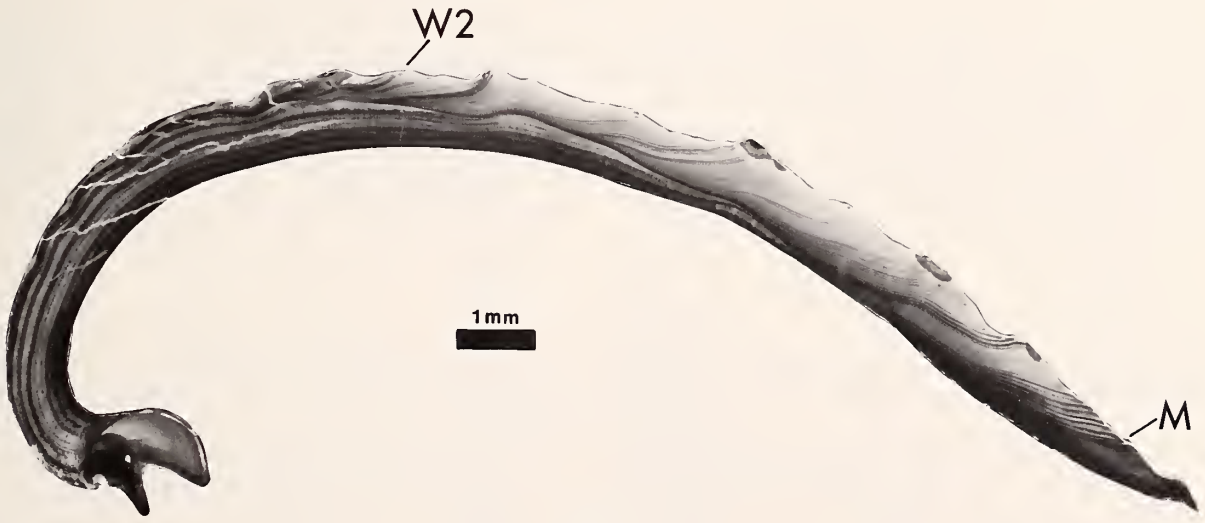

Figure 10

Photographic enlargement of a thin shell section of a specimen of *Corbicula fluminea* collected from the cage at station AC on 20 October 1982. Growth cessation marks are labelled as in Figure 9. Note differences in post-move shell growth between this clam and the one collected from the control station (Figure 9). Total shell height is 15.7 mm; growth is to the right.

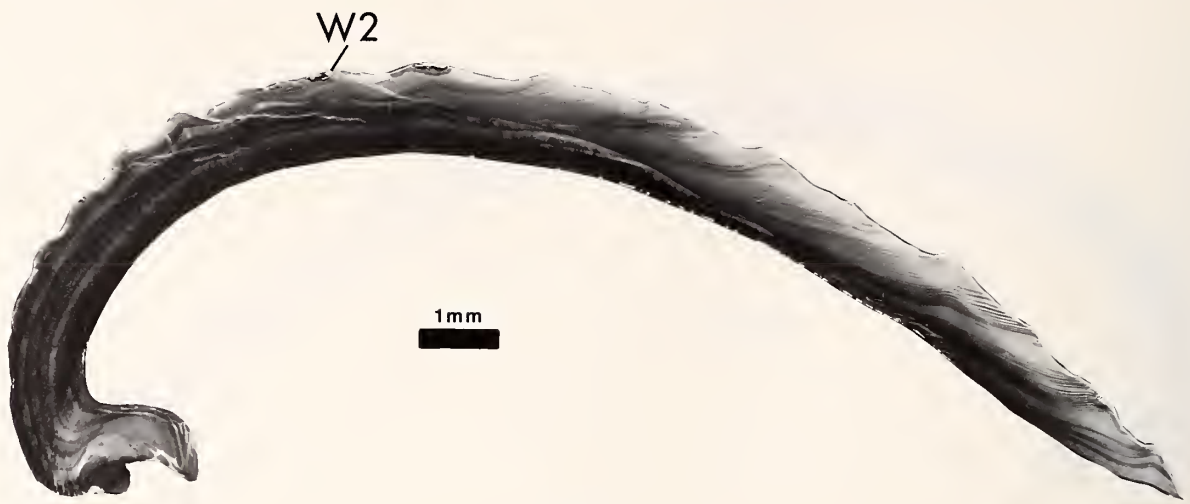

Figure 11

Photographic enlargement of a thin shell section of a specimen of *Corbicula fluminea* collected from the natural population at station C on 20 October 1982. Growth cessation mark is labelled as in Figure 9. Total shell height is 15.5 mm; growth is to the right.

stations, any differences in shell growth between groups subsequent to the move would most likely be due to site-specific factors. As previously stated, the growth disturbance associated with the move and placement in cages in 1982 had a much less deleterious effect on subsequent growth than did notching the ventral shell margins in 1981 (compare Figure 9 with Figures 3-5). Shell deposited after the notch resembled the immediate post-move shell in that both were relatively opaque in thin section and growth rates (μm/increment) were depressed. Median shell growth from W2 to the shell margin in three of the six collections (30 July, 27 August, and 17 November) was considerably greater in wild clams than those from control stations, but this was most likely a result of the smaller mean shell height at W2 in the wild clams collected on these dates (Table 5). Counts of microgrowth increments from W2 to the shell margin in clams from control stations DI and C were not significantly different from counts in the same shell region in clams from the natural population ($F = 1.11$, $P > 0.25$; Table 5; Figure 12). Furthermore, the number of increments counted from W2 to the shell margin in the four collections through October (or those collections before which water temperatures were greater than 10°C) suggests an average deposition rate of one increment per day. A linear regression of the pooled counts from wild and control clams against days since 19 July 1982 resulted in a slope (1.18) that was not significantly different from 1.00 ($t_s = 1.52$, $P > 0.2$; $n = 28$, $r^2 = 0.86$; see Figure 12).

From 19 July 1982 to the date of collection, clams moved to experimental station AC grew slower and deposited fewer increments than caged clams at control stations (Table 6). A linear regression of increments from M to the shell margin against days since 19 July in clams collected from the control stations through October resulted in a slope (0.97) which was not significantly different from

Table 4

Shell growth and number of microgrowth increments from the winter 1981-1982 growth cessation mark (W2) to the growth cessation mark caused by the move (M) on 19 July 1982 in specimens of *Corbicula fluminea*. Collections from all dates were pooled.

		Shell growth (μm)		Number of microgrowth increments		
Station	N	Median	Range	Mean	±95% CI	Range
DI	17	5390	3640-9290	115.0	108.6-121.4	99.3-139.3
C	15	5260	3210-6810	112.6	101.1-124.1	79.7-162.3
AC	13	3880	2015-9940	114.1	100.0-128.2	81.7-150.3
Total	45	5150	2015-9940	113.9	108.3-119.5	79.7-162.3

Table 5

Shell growth and number of microgrowth increments from W2 (see Table 4) to the shell margin in specimens of *Corbicula fluminea* collected on six dates in 1982. Collections from stations DI and C were from cages, while those from NP were from the natural population at station C.

Date of collection	Station	N	Mean shell height at W2 (mm)	Shell growth (μm)		Number of microgrowth increments	
				Median	Range	Mean	Range
30 Jul	DI	3	7.6	5310	4280–5680	125.1	112.0–137.3
	C	3	8.7	3585	3560–5640	110.4	94.3–132.0
	NP	2	6.1	7000	6310–7690	120.7	115.7–125.7
27 Aug	DI	2	8.0	7300	5960–8650	147.5	142.7–152.3
	C	2	8.7	5740	5350–6140	145.8	142.0–149.7
	NP	2	2.9	12,530	11,310–13,750	149.0	142.3–155.7
23 Sep	DI	3	8.8	8740	8440–8820	171.8	165.3–175.7
	C	2	8.6	8390	7900–8880	186.0	176.7–195.3
	NP	1	6.6	7620		138.7	
20 Oct	DI	3	8.1	10,280	7460–12,340	220.7	213.0–235.7
	C	2	6.2	10,720	10,690–10,740	193.5	193.0–194.0
	NP	3	6.9	10,060	9250–12,250	231.4	218.7–238.3
17 Nov	DI	3	8.4	9430	9400–9450	222.9	214.3–230.3
	C	3	9.0	9380	8380–10,440	221.9	211.7–231.7
	NP	3	5.9	12,000	10,000–13,120	234.6	215.7–271.7
15 Dec	DI	3	6.6	11,010	10,320–14,150	246.5	234.7–268.7
	C	3	8.0	9310	8750–11,120	256.1	217.3–290.3
	NP	3	6.3	11,250	10,620–13,250	247.0	232.0–266.3

1.00 ($t_s = -1.36$, $P > 0.2$; $n = 24$, $r^2 = 0.98$). However, a similar linear regression based on counts from clams collected from station AC had a slope (0.79) that was significantly lower than 1.00 ($t_s = -3.03$, $P < 0.02$; $n = 10$, $r^2 = 0.94$; see Figure 13A). This strongly suggests that, on the average, clams at station AC were growing on fewer days than those at stations DI and C. Furthermore, both the absolute amount of shell growth (Figure 13B)

Table 6

Shell growth and number of microgrowth increments from M (see Table 4) to the shell margin in specimens of *Corbicula fluminea* collected from cages at the three stations on six dates in 1982.

Date of collection	Station	N	Shell growth (μm)		Number of microgrowth increments	
			Median	Range	Mean	Range
30 Jul	DI	3	450	390–550	14.3	12.3–18.0
	C	3	350	220–380	14.3	13.3–15.0
	AC	3	230	170–310	15.1	14.7–15.3
27 Aug	DI	3	2320	2300–3220	41.3	40.0–42.3
	C	3	2080	1800–5720	38.7	38.0–39.7
	AC	2	440	160–570	29.5	22.7–36.3
23 Sep	DI	3	3340	3120–3530	68.6	61.3–76.7
	C	3	2750	2700–3560	64.2	63.3–65.0
	AC	2	1520	1310–1740	60.0	56.3–63.7
20 Oct	DI	3	3580	3320–4080	94.5	91.3–96.3
	C	3	4620	4090–5810	94.0	90.7–96.0
	AC	3	1530	820–2000	78.1	67.0–84.0
17 Nov	DI	3	4060	3960–4390	99.4	91.3–105.3
	C	3	3500	3370–3620	108.0	104.7–110.3
	AC	1	1660		88.3	
15 Dec	DI	3	5220	4910–5330	129.6	128.0–131.0
	C	3	3880	3500–4620	123.2	119.3–128.0
	AC	3	950	870–1000	58.8	53.0–61.7

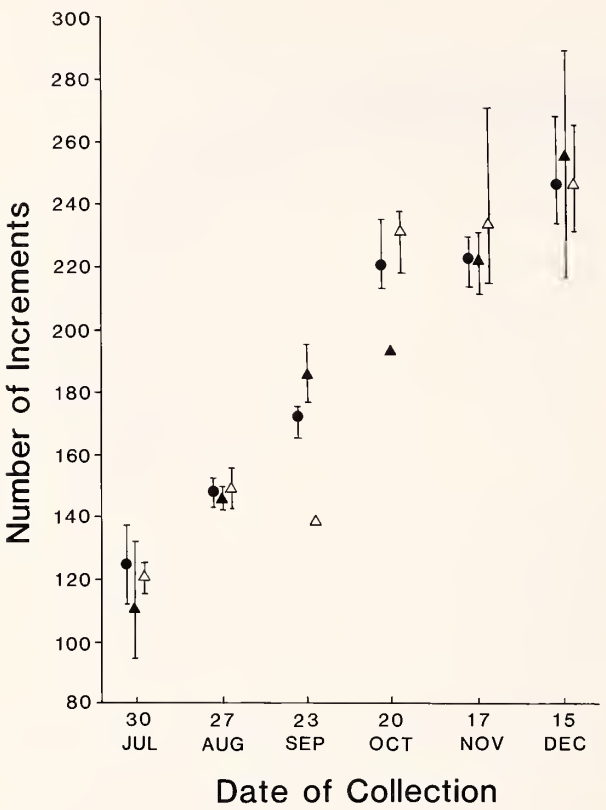

Figure 12

Mean (symbols) and range (vertical lines) of the number of microgrowth increments from the winter 1981–1982 growth cessation mark (W2; see Figures 9–11) to the shell margin in specimens of *Corbicula fluminea* collected from cages at stations DI (solid circles) and C (solid triangles) and from the natural population at C (open triangles) in 1982. Date of collection is plotted three days before actual date for station DI and three days after for the natural population to permit plotting (see Table 5).

and growth rate (Figure 13C) were lower in clams at AC than at the control stations. Post-move growth rates during the first 11 days (or through 30 July) at all stations were lower than pre-move rates. This may have been due to a period of acclimation to the site and(or) cage, and may also be related to deposition of the opaque region immediately ventral to M by control clams. Growth rates at control stations DI and C returned to pre-move levels by the August sample, while those at AC were lower than pre-move rates in all subsequent samples (Figure 13C). Evidence strongly suggests that the effluent discharged near station AC decreased the number of days of growth as well as growth rates of specimens of *Corbicula fluminea* relative to those at control stations.

DISCUSSION

In the present study, we have shown that microgrowth increments in the outer fine crossed-lamellar shell layer of *Corbicula fluminea* (described previously by Prezant & Tan-Tiu [1985]) were formed at the rate of approximately one per day and can be used to date shell regions. Furthermore, cessation of growth in winter resulted in a growth discontinuity within the inner complex crossed-lamellar layer and a growth cessation mark in the outer layer. Periodically deposited growth patterns in the two shell layers and evidences of growth cessations were used to reconstruct the growth history of groups of *C. fluminea* exposed to natural and anthropogenic environmental perturbations. Other methods, such as examination of external shell growth lines or serial measurements of shell axes (length or height) may not have been sensitive enough to document these changes in such short-term monitoring studies.

The periodicity of formation of microgrowth increments in outer prismatic or crossed-lamellar layers of several other bivalve species has been investigated previously by a number of researchers (see Lutz & Rhoads, 1980). In the most commonly analyzed species, *Mercenaria mercenaria,* several investigators have documented a solar daily periodicity of formation in subtidal populations (Pannella & MacClintock, 1968; Kennish & Olsson, 1975; Thompson, 1975; Kennish, 1980; Fritz & Haven, 1983), but there is also evidence that suggests a closer correlation with the lunar day in intertidal specimens (Pannella, 1976). Tidally deposited growth increments have also been observed in intertidal populations of *Cerastoderma edule* (Richardson *et al.,* 1979) and *Clinocardium nuttalli* (Evans, 1972). Longer cycles, such as seasonal changes in temperature, are often reflected (and most easily discerned) in middle and inner shell layers, such as those of *M. mercenaria* (Fritz & Haven, 1983), *Mya arenaria* (MacDonald & Thomas, 1980), and *Mytilus edulis* (Lutz, 1976). Similarly, in *Corbicula fluminea,* short cycles (days) are reflected in outer layer microgrowth increments and long cycles (seasons) in inner layer growth discontinuities.

Caution must be exercised in using growth patterns to reconstruct life histories of individual specimens. This is due to both subjectivity in the method of detecting and counting increments (Crabtree *et al.,* 1979/1980; Hughes & Clausen, 1980) and natural variability within a bivalve population in growth rate (*i.e.,* number of increments deposited and their width in a specified time) due to age and individual differences in sensitivity to environmental stresses (Kennish & Olsson, 1975; Crabtree *et al.,* 1979/1980; Richardson *et al.,* 1980; Fritz & Haven, 1983). This does not imply, however, that attempts to interpret growth patterns in bivalve shell structures should be avoided. On the contrary, use of growth patterns in carbonate and proteinaceous secretions to determine age, growth rates, and aspects of life history of both vertebrates and invertebrates is well founded in studies of population dynamics and ecology (see Ricker, 1975). One strives to be as accurate as possible by analyzing large numbers of shells, applying objective criteria to the defi-

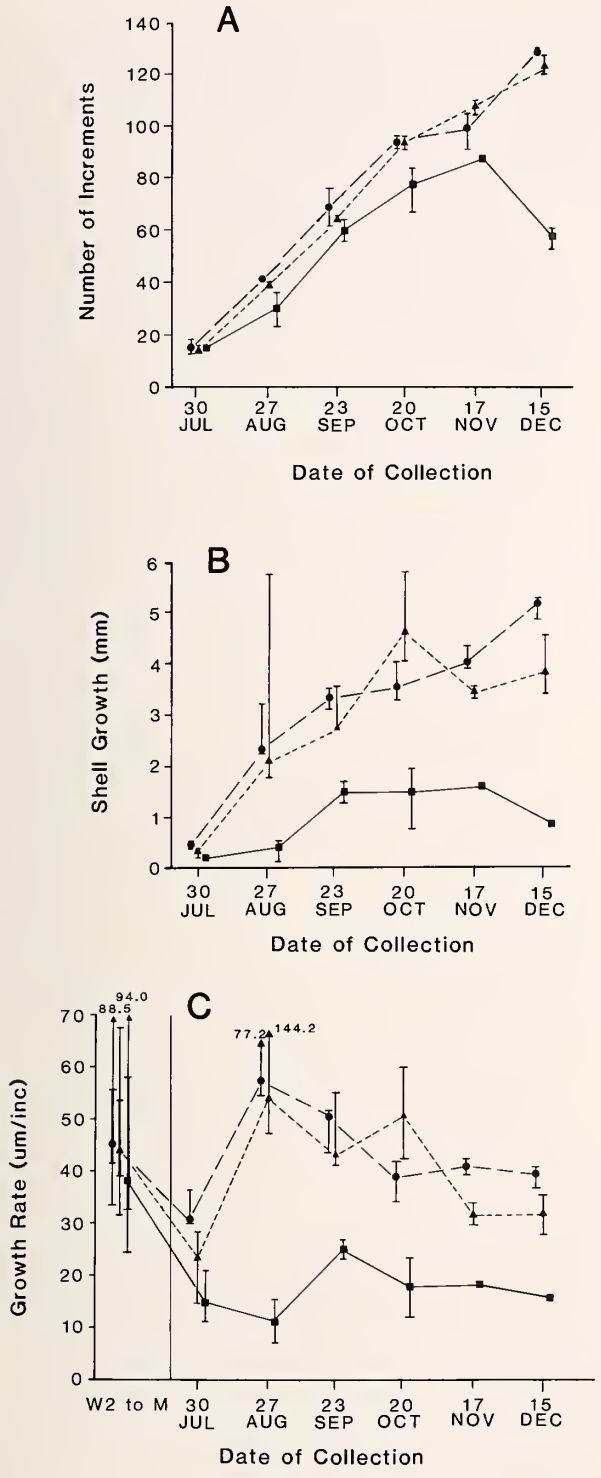

Figure 13

Analyses of shell growth of specimens of *Corbicula fluminea* at stations DI (circles and long dashed lines), C (triangles and short dashed lines), and AC (squares and solid lines) from the growth disturbance mark caused by the move on 19 July 1982 (M; see Figures 9 and 10) to the shell margin (date of collection). Offset on X-axis is the same as in Figure 12 (see Table 6). A. Mean (symbols) and range (vertical lines) of number of microgrowth increments. B. Median (symbols) and range (vertical lines) in shell growth. C. Median (symbols) and range (thin vertical lines) in growth rate (μm/increment). Also shown are distributions of growth rates from W2 to M (or prior to the monitored growth phase) in each group. Top and bottom of heavy bar are 75th and 25th percentiles, respectively, of the distributions of pre-move growth rates.

nition of increments and patterns in shell sections (such as those of Crabtree *et al.*, 1979/1980), and being consistent in interpretation and analysis.

Kennish & Olsson (1975) were the first to use bivalve shell growth patterns to monitor environmental perturbations. Growth cessation marks, a decrease in microgrowth increment width, and "replacement" of prismatic with "crossed-lamellar" microstructures in the outer layer of specimens of *Mercenaria mercenaria* were directly correlated with increased exposure to elevated water temperatures from a nuclear power plant. In the present study, the number of days of growth and shell growth rates of specimens of *Corbicula fluminea*, as measured through analyses of microstructural banding patterns, decreased (relative to controls) with exposure to the combined effluents from chemical and sewage treatment plants. Results of a concurrent *in situ* study of physiological responses to the effluent (Cantelmo-Cristini *et al.*, 1983) support these observations. In 1982, Cantelmo-Cristini *et al.* (1983) measured total adenylates and calculated adenylate energy charge of each of the specimens whose shells were sectioned for growth analysis in the present study. Energy charge of specimens was lower at station AC than at the control sites on 7 of 9 sampling dates during the monitored period, an indication of a site-specific stress at AC which was, most probably, chronic exposure to the effluent.

It is common in shell growth studies of this nature (*e.g.*, Richardson *et al.*, 1980; Fritz & Haven, 1983) to notch the ventral shell margin to induce a size-time benchmark in shell microstructure. As shown in the present study, notching should be avoided because it caused a decrease in growth rate and alteration of shell microstructure in the 1981 group. Alternative methods of inducing a growth cessation mark in shell microstructure, such as thermal shock (Richardson *et al.*, 1979; Fritz & Haven, 1983) or moving the animal to a new location (Fritz & Haven, 1983; this study) cause less alteration to shell microstructure and apparently less damage to mantle tissue.

Size-specific growth rates of *Corbicula fluminea* in the Raritan River, New Jersey, were slower than those measured in Lake Benbrook, Texas, for periods of similar duration (Britton *et al.*, 1979). In the present study, mean growth rates along the length axis in spring and summer of 1981 and 1982 (periods of 136 and 160 days in 1981 and 114 days in 1982) were 63 and 55 μm/day, and 46 μm/day, respectively, for uncaged clams with ini-

tial shell lengths ranging from 4.2 to 12.3 mm. In Lake Benbrook, the mean growth rate of specimens held in containers for 107 days was 54 μm/day, but initial shell lengths ranged from 10 to 25 mm. Measured growth rates in the two studies were similar, but the larger initial shell lengths of clams in the Texas study, and the fact that smaller clams tend to grow faster than larger clams (BRITTON *et al.,* 1979) indicated that size-specific growth rates were slower in the Raritan River. This difference may actually be greater because container-held specimens tend to grow slower than uncaged individuals (BRITTON *et al.,* 1979).

The largest specimen of *Corbicula fluminea* collected to date from the Raritan River is 25 mm in shell length and was found dead in March 1981 (TRAMA, 1982). The largest specimen analyzed in the present study was 20.8 mm in shell length at the end of its second growing season (age 1+ years). Consequently, it is likely that the 25 mm specimen was between 2 and 3 years old at the time of death, and not 3 to 4 years old as concluded by TRAMA (1982), which changes the latest possible year in which the species became established in the Raritan River system to 1979 instead of 1978. The relatively small maximum size and slow size-specific growth rates may result from low temperatures and(or) their duration in winter, because the Raritan River is the northernmost extension of the recorded range of *C. fluminea* along the Atlantic seaboard (TRAMA, 1982). However, other factors such as food supply and quality, bottom type, and flow regime may also be involved in creating a "dwarfed" population. Causes of the catastrophic mortalities of *C. fluminea* observed in the Raritan River (and in other lotic systems [BRITTON & MORTON, 1982]) are also not known. Research into causes of "dwarfism" and mortalities would be a logical direction for future studies of the population dynamics of *C. fluminea* in the Raritan River.

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